Morphological comparison of the buccal apparatus in two bivalve commensal Carapidae

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Figure 2

Introduction

Several species of the Carapidae (figure 1) are well known to have commensal or parasitic relationships with invertebrates (Trott 1970, Markle and Olney 1990). *Carapus acus* (Brunnich, 1768), *Encheliophis boraborensis* (Kaup, 1856), and *Encheliophis homei* (Richardson, 1844) display carnivorous traits, enabling them to ingest hard prey: the buccal parts are robust, the dentition is well developed, the mouth opens widely, and the premaxillaries can project slightly frontwards. (Parmentier *et al.* 1998).

The three species of the genus *Onuxodon* and the species *Encheliophis dubius* (Putnam, 1874) are the only Carapidae species known to live principally in bivalves (figure 2), between the mantle and the shell.

In this study the diets, cephalic skeletons, and musculatures of *O. fowleri* (Smith, 1955) and *E. dubius* (Putnam, 1874) are compared with each other. The aim is to compare the cephalic morphology of both species to see how it responds to the demands of their particular way of life (bivalve host and diet).


Figure 1

Materials and methods

27 *O. fowleri* specimens (TL : 57 to 90 mm) were collected in Hansa Bay (Bismarck Sea) in Papua New Guinea. They were found in representatives of *Pinctada margaritiferae* (Linné, 1758) (Bivalvia, Pteriidae). The morphological data pertaining to *E. dubius* (TL : 90-120 mm) were compiled from specimens from the following institutions: AMNH, CAS, LACM, SIO and UF. The cephalic structures were alizarin-stained, dissected, examined, and drawn with the help of a coupled binocular (Wild M10).

The stomach contents of 23 *O. fowleri* specimens were collected. Dr Castro-Aguirre and Garcia-Dominguez (CICIMAR, Mexico) realised the diet determination of 17 *E. dubius* specimens (TL: 91-108 mm) from Espiritu Santo Island (Gulf of California, Pacific Ocean).

To compare the cephalic structures of the two species, we referred their neurocrania to a same reference length: the distance between the mesethmoid and the basioccipital..

Results

I. Stomach contents

O. fowleri. Among the 23 digestive tracts examined, 9 were empty, 3 contained remains of Ostracoda and Amphipoda, 8 contained remains of Annelida, 2 contained unidentifiable soft tissues. The preys appeared to be shredded.

E. dubius. Among the 17 stomachs examined, 6 were empty, 11 contained Amphipoda and/or Mysidae. One contained Annelida remains.

II. Skull

The cephalic skeleton of *E. dubius* has the same bony components as that of *O. fowleri*; the differences between the crania of these two species lie in the dentition, proportions, arrangement, and shape of their components.

O. fowleri.

II.A ***Onuxodon fowleri*** (figure 3)

The maximum height of the neurocranium represented about 45% of the length between the mesethmoid and the basioccipital The anterior parts of the maxillaries and premaxillaries are situated beneath the mesethmoid. The premaxillaries have no ascending process. Their lateral process is extended at the front and pierced by a large foramen into which the large tooth of the corresponding dentary penetrates. The hyomandibular double joint with the neurocranium slants forward. The two condyle heads of the articulation facet of the hyomandibular with the neurocranium are extended by thickenings that converge towards a third thickening in continuation of the symplectic. The quadrato-mandibular joint is situated at the level of the centre of the joint between the hyomandibular and the neurocranium, the operculum and subopercullum are smaller (16% of the suspensorium).

Dentition : 1) The vomer bears a set of small conical teeth. 2) The premaxillaries and dentaries each bear a broad, backward-curving tooth, separated by a diastema from small conical teeth. 3) the palatine possess several rows of small conical teeth.

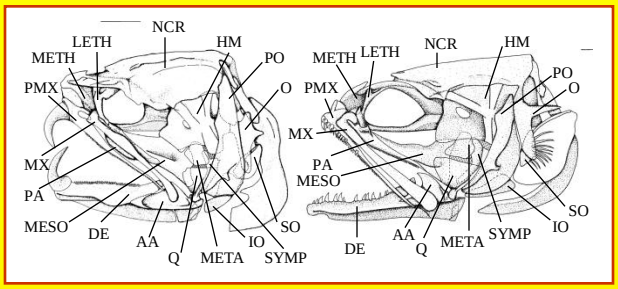

Figure 3: Lateral view of the cephalic skull of *Onuxodon fowleri* (A) and *E. dubius* (B). The suborbital range and branchiostegal rays are not represented.

II.B *Encheliophis dubius.*

(Figure 3)

The neurocranium of *E. dubius* is less elevated than that of *O. fowleri* (its height represents approximately 30% of the length of the cranium). Unlike the latter, it possesses a convex mesethmoid. The joint between the maxillary and premaxillary lies in front of the ethmoid region. The anterior part of the suspensorium (palatine, mesopterygoid) is situated further to the front. The joint between the hyomandibular and the neurocranium is almost horizontal. The hyomandibular thickening and the neurocranium are at the same distance from the parasphenoid, but they are further apart in *E. dubius* (the angle hmt1/hmt2 measures about 80°) than in *O. fowleri*. Furthermore, the ventral thickening of the hyomandibular (hmt3) is almost vertical in *E. dubius* and has a backward orientation in *O. fowleri* . The quadrato-mandibular joint lies beneath the anterior condyle of the hyomandibular at its joint with the neurocranium The opercle is more developped (40% of the suspensorium) and the preoperculum is tilted.

Dentition : 1) The premaxillary displays, at the front, a short row of external cardiform teeth and two more internal anterior conical teeth that curve inwards. They are followed by four unequal rows of small teeth. 2) The dentary displays an external row of backward- and inward-curving conical teeth, and three internal rows of small teeth similar to those of the premaxillaries. 3) The palatine possess several rows of small conical teeth.

III. Musculature

Few differences exist in the composition of the upper jaw musculature. The division into bundles of the *adductores mandibulae* is the same in both species. With a smaller neurocranium and with the coronoid processes lying further to the front, the fibres of adductors A2, A2, and A3 insert lower on the neurocranium and generally tilt more markedly backward. (figure4)

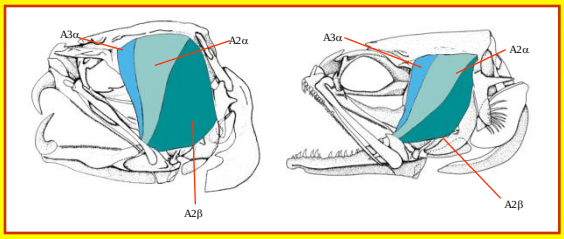

Figure 4 : Left lateral view of the head musculature A2α: adductor mandibulae A2α, A2α : adductor mandibulae A2α, A3β : adductor mandibulae A3β

Discussion

A widely cleaved mouth, a well-developed dentition, a reinforced hyomandibular, robust jaws, and a powerful musculature confirm the carnivorous diet revealed by the stomach contents. The aquatic diet intake is normally characterised by a depression that causes a water flow and consequently a suction. The latter is more efficient when the buccal cavity is shaped like a large cone with a small circular mouth opening. From this point of view, the suction exists but is probably weak in both species because the mouth remains broadly split. The small buccal cavity, the remote quadrato-mandibular, the peculiar dentition, the narrow operculum suggest that *O. fowleri* should be better at grasping its preys. Moreover, the characteristic position of the upper jaw beneath the ethmoid region determines a firm fulcrum on the neurocranium that should facilitate penetration of the large teeth into the prey when the mouth closes. The skeletal, muscular, and ligamentary organisation of the *E. dubius* head is as described by Parmentier et al. (1998) for the commensal Carapini *E. homei*, *E. boraborensis*, and *C. acus*. As these fish *E. dubius* can open its mouth widely with slight protrusion of the premaxillaries. This system seems better adapted to a feeding mechanism where sucking would have a more important role.

The difference of mouth opening strategy between both speices is reinforced by the position and the orientation of the A3α, A2α, and A2β. The efficiency of muscle contraction is maximal when the muscles are perpendicular to the axis passing through their insertion on the jaw and the joint between the jaw and the quadrate (Turingan 1994). Figure represents schematically the average orientations of bundles A3α, A2α, and A2β and the orientations of the insertion-joint axes (axis 1 for A3α and axis 2 for A2α and A2β) for five mandible positions. In *O. fowleri*, the average orientation of the A2α fibres is perpendicular to axis 2 when the mouth opening is between 45° et 30°, that of A3α is perpendicular to axis 1 when the opening is between 30° and 15°, and that of A2β is perpendicular to axis 1 when the mouth is closed. In *E. dubius*, only A2α can be almost perpendicular to the corresponding axis (axis 2), and solely when the mouth is closed. From this point of view, in *O. fowleri*, the general more erected orientation of A2α, A2β and A3α bundles is thus better adapted to the necessity of seizing their preys when the mouth closes.

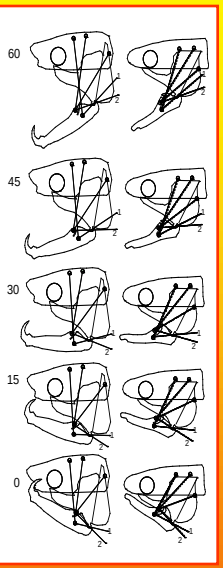

Figure 5 : Diagram showing the average positions of bundles A3, A2 et A2 at five stages as the mouth closes. Full lines: *O. fowleri*; dotted lines: *E. dubius*

Any change in the size or position of a component can affect partly or entirely the organisation of the skull and its biomechanics (Gosline 1987; Galis and Drucker, 1996). In this context, it is possible to formulate a model regarding the transformation of a buccal system like that of *E. dubius* into that of *O. fowleri*. The suspensorium can be divided into two parts: (1) a posterior part consisting of the hyomandibular, the metapterygoid, the symplectic, the quadrate, and the preopercular, and (2) an anterior part including the palatine and the mesopterygoid. If the posterior part of the *E. dubius* suspensorium undergoes a rotation of approximately 19° around the posterior joint between the hyomandibular and the neurocranium, and if simultaneously the palatine and mesopterygoid slide horizontally along the neurocranium, the resulting new suspensorium can be brought to coincide with that of *O. fowleri*. These displacements in *E. dubius* have additional consequences: (1) the jaws are pulled backward, the upper jaw sliding beneath the ethmoid region, (2) the preopercular becomes more erect, (3) the volume of the buccal cavity is reduced. Applied to A2α, A3α, and A2β, however, a 19° rotation brings these bundles to a more erect position without making them coincide with those of *O. fowleri*. The causes of such modifications are difficult to explain but the latter could be revealing a mechanism of the biodiversity.

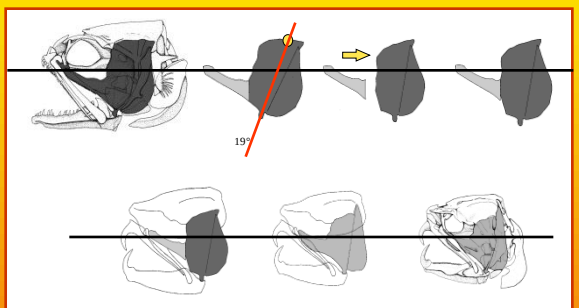

Figure 6 : Imagined transformation of the *E. dubius* suspensorium (A) leading to a suspensorium like that of *O. fowleri* (B). Line : floor of the neurocranium; open circle: point around which the suspensorium is rotated.

Conclusion

1) Although the cephalic morphology is different in *E. dubius* and *O. fowleri*, the same types of prey are found in their stomachs. Like the holothuroid commensal Carapini, *O. fowleri* and *E. dubius* eat crustaceans and annelids. Consequently, differences in the seizing prey apparatus are not necessarily related to different diets but it could reflect strategies of prey seizing adapted to the same type of prey (Kotrschal 1989 ; Turingan 1993).

2) The buccal anatomy of these species seems more dependent on the different diet constraints than the occupation of a particular host.

3) The model could be indicative of how structure modifications and their influences on annex pieces could in part have a role in the biodiversity.

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